POST-FIRE REGENERATION OF KRUMMHOLZ WHITEBARK PINE: A CONSEQUENCE OF NUTCRACKER SEED CACHING

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Abstract

The potential for post-fire forest regeneration was studied in a 2 ha subalpine burn on Cathedral Peak in Yosemite National Park. The pre-fire forest was a pure stand of krummholz whitebark pine, *Pinus albicaulis.* Data on stand characteristics, seedling density, height, cluster size, and seedling micro-habitats were collected from five 2 × 168 m belt transects. Three additional transects, 2 × 61 m or 2 × 76 m, located in the contiguous, unburned forest provided comparative data. Observations and circumstantial evidence suggest that Clark's Nutcracker, *Nucifraga columbiana,* a bird that buries pine seeds habitually, has initiated the early stages of *P. albicaulis* regeneration on the burn.

In the Sierra Nevada of California, the majority of subalpine fires are caused by lightning strikes, which typically consume less than 0.1 to 0.5 ha of forest (based on records from District Offices or Headquarters of the 8 National Forests and 3 National Parks within the range). Fires that consume larger areas are highly unusual in this range. A lightning strike on 8 August 1975 ignited a fire on Cathedral Peak, Yosemite National Park, and burned approximately 2 ha on the upper west slope. Before the fire, the burned tract was covered by a pure stand of krummholz whitebark pine, *Pinus albicaulis* Engelm., referred to as the elfinwood form (Clausen 1965). In this ecotype, trunks and branches grow close to the ground, forming dense, creeping mats of pine.

Whitebark pine occurs primarily as a climax species in the Sierra Nevada and, consequently, does not depend on fire for regeneration (S. F. Arno, pers. comm.). In the Rocky Mountains of Montana and Wyoming, however, whitebark pine is a climax species on high, exposed sites and successional in more favorable subalpine environments (Lanner 1980, Arno pers. comm.). Seral stands and mixed associations are periodically regenerated by severe fires and surface fires, respectively (Arno pers. comm.).

The question of whitebark pine regeneration in krummholz stands is of particular interest relative to the 1975 fire. The cones of whitebark pine are indehiscent (but not serotinous) and thus do not open when ripe. The seeds are large and wingless. Previous studies (Tomback 1978, 1982, Hutchins and Lanner 1982) have demonstrated that most seed dispersal is effected by Clark's Nutcracker, *Nucifraga*

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columbiana Wilson, a bird of the family Corvidae. Each fall, one bird may bury as many as 32,000 whitebark pine seeds in caches (i.e., separate clusters) of 1 to 15 seeds, with a mean of 3.7 seeds per cache (Tomback 1982). A common growth form of erect whitebark pine is multi-trunked; a single tree may consist of two or more trunks often partly fused at the base, suggesting that this growth form originates from nutcracker caches. Supporting this hypothesis, the analysis of Linhart and Tomback (1985) indicated that several to all trunks of a multi-trunked tree have distinct genotypes.

Post-fire forest regeneration of the erect form of limber pine, *Pinus flexilis* James, another large-seeded, wingless species, was shown by Lanner and Vander Wall (1980) also to be the consequence of seed storage by Clark's Nutcracker, an important disperser for this species (Tomback and Kramer 1980, Lanner 1980). Because krummholz forms of conifers are noted for low seed productivity and germination potential (Tranquillini 1979), the process of forest regeneration might be slow despite the participation of nutcrackers. It is of interest that the Eurasian Nutcracker, *N. caryocatactes* L., is a disperser of the Japanese stone pine, *P. pumila* Regel, a relative of whitebark pine that occurs only in krummholz form (Mezhenny 1961, 1964). The Cathedral Peak burn provided a unique opportunity to examine 1) the pre-fire composition of the forest community, 2) if and how much forest regeneration had occurred by 1979, 3) the conditions under which regeneration occurred, and 4) whether Clark's Nutcrackers or other sources were responsible for regeneration.

Study Site

The burn occurred near the top of the west slope of Cathedral Peak, Yosemite National Park, elevation 3337 m, approximately 37°55′N and 119°25′W, in Mariposa and Tuolumne Cos., California. A right triangle in shape, the burned tract runs parallel to the ridgetop for 200 m at 3295 m elevation and ends at 3210 m elevation. Slope aspect is nearly due west; the slope angle increases from 25° to 29° near the lower limit of the burn. The substrate is predominantly granitic gravel with occasional patches of duff.

In the center of the burn, on the ridgetop, and on the northern boundary, a few trees escaped fire damage. The southern boundary interfaces with an unburned stand of krummholz *P. albicaulis* that is a maximum of 80 m long in the north–south direction. This stand terminates abruptly above a talus-filled gorge. All burned trees in the study site were killed and defoliated, but the charred skeletons of the krummholz pine generally remained intact. In a few places, however, the fire had burned with such intensity that the trees were reduced to charred pieces.

TABLE 1. DESCRIPTION OF TRANSECTS ON CATHEDRAL PEAK AND DATA COLLECTED.

Transect	Elevation (m)	Length (m)	Data collected
1	3290	168	*In burn:* No. trunks/tree, density of trees, old and new cones, density of seedlings, no. of seedlings per cluster, seedling heights, seedling micro-habitats.
5	3218	122	
2	3274	168	*In burn:* Density of seedlings, no. of seedlings per cluster, seedling heights, seedling micro-habitats.
3	3260	168	
4	3253	168	
6	3290	61	*In live stand:* Density of seedlings, no. seedlings per cluster, seedling heights, seedling micro-habitats, new and old cones.
7	3276	61	
8	3256	76	

Below 3170 m on the west slope of Cathedral Peak, small stands of the typical, erect growth form of whitebark pine occur. The east slope of the peak is forested densely by whitebark pine, the erect growth form giving way to krummholz near the top of the slope.

METHODS

In August and September of 1979, data were gathered from a series of 2 m wide belt transects parallel to the ridgetop in order to describe the pre-fire forest and rate of regeneration. A random numbers table was used to select the starting point elevation for each transect. Transects one and five were completed on 9 and 10 August, transects two to four on 8 and 9 September, and transects six to eight on 9 September. Transects one to five were run through the burned tract with one and five near the upper and lower boundaries, respectively. Transect five is shorter than the others by 46 m to exclude a section where the fire had reduced the trees to charred logs. Transects six, seven, and eight were run through the contiguous, unburned stand. Description of transects and type of data collected are presented in Table 1.

Trunk diameters were measured 0.3 m from the base of the largest trunk on each tree. Whitebark pine seedlings were identified by either number of needles per fascicle (i.e., 5) or the number of cotyledons (7 to 9, Mirov 1967). Seedling heights were measured from the substrate to the tip of the woody stem. All seedlings originating within a circle 5 cm in diameter were defined as one cluster and on one 'site'; diameters of seedling sites (i.e., area containing all seedlings of a cluster) were noted. (No two sites occurred close enough to cause confusion.) Two clusters of seedlings taller than 15 cm were encountered on the transects and probably originated before the fire. Other seedlings were considered to originate post-fire, because whitebark pine, like most arid-site conifers, is likely to be slow-growing

(Fritts 1974). Seedlings were not aged by growth increments, but to test their probable post-fire origin their heights were compared to those of seedlings germinated in August 1975 near Reds Lake on Mammoth Mountain, Inyo National Forest, Mono Co., California at an elevation of 2830 m, and less than 40 km straightline distance southeast from Cathedral Peak (Tomback 1982).

The activities of Clark's Nutcrackers were observed near and on both slopes of Cathedral Peak. In relation to these activities, the numbers and conditions of new and old whitebark pine cones on east and lower west slope trees were censused along base to peak line transects and reported in detail in Tomback (1981).

Non-parametric and parametric tests used for data analysis are from Siegel (1956) and Bailey (1959), respectively. Standard deviations (s.d.) are reported with means.

Results

Pre-fire stand characteristics. As indicated by the tree skeletons on transects one and five, most of the trees had been multi-trunked, with trunks fused at the base with clear lines of demarcation between trunks. Each multi-trunked entity is counted here as a single tree cluster. Between transects one and five there were no significant differences in sample distributions of number of trunks per tree cluster or trunk diameters ($d = 0.0$ and $d = 0.06$, respectively, Normal Distribution Significance test). The overall number of trunks per tree cluster ranged from one to five with a mean and median of 2.2 ± 1.08 and two trunks per tree cluster, respectively. Diameters of trunks ranged from 4 to 43 cm ($\bar{x} = 14.6 \pm 6$ cm, median = 13 cm) (Table 2). Before the fire, the density of krummholz whitebark pine trees was 0.131 trees (each 'tree' may be a cluster or single-trunk form) per m^2 of transect one and 0.168 trees per m^2 of transect five (Table 2).

Seedlings. Data on post-fire seedling establishment were provided by transects one through five for a total survey distance of ca. 790 m (Table 3). Along these transects were a total of 31 seedling sites, represented by 16 solitary seedlings and 15 seedling clusters, with all seedlings below 15 cm in height. It must be emphasized that the stems of the seedlings in a cluster were separate down to the root; thus, each seedling was a distinct individual, and clusters were not produced by branching of a single seedling.

The combined density of solitary seedlings and seedling clusters per transect ranged from $0.015/m^2$ to $0.027/m^2$, with an overall mean density of $0.020/m^2$. The number of seedings per cluster ranged from one to four with an overall mean, s.d., and median of 2.6 ± 0.74 and two seedlings per cluster, respectively. There were no significant differences in the number of seedlings per cluster among the

TABLE 2. PRE-FIRE STAND CHARACTERISTICS AND CONE PRODUCTIVITY OF LIVE TREES IN BURN.

	Transect 1	Transect 5
Burned trees		
No. of trees	36	41
Tree density/m^2	0.131	0.168
No. trunks/tree		
Range	1–5	1–4
Mean	2.2	2.2
s.d.	1.1	1.1
Median	2	2
Trunk diameter (cm)		
Range	4–43	6–30
Mean	15.1	14.2
s.d.	7.6	5.0
Median	14	13
Live trees		
No. of trees	10	3
With new cones	0	0
With old cones	2	0

five transects (t-test) (Table 3). The seedlings in a cluster originated either from nearly the same point (0.0 cm diameter) or within a circle of 5 cm diameter ($\bar{x} = 1.7 \pm 1.7$ cm diameter, median = 1 cm diameter). The overall mean and median number of seedlings in one site were 1.7 ± 0.96 and 1 seedling, respectively (Table 3).

Seedling heights ranged from one to 13 cm ($\bar{x} = 3.9 \pm 2.6$ cm, median = 3.0 cm, n = 54 seedlings). Among the five transects, mean seedling heights ranged from 2.0 cm to 5.3 cm (Table 3). Only between transects three and four were seedling heights significantly different ($t = 3.3$, $df = 22$, $0.002 < P < 0.01$).

Two sites with recently germinated seedlings were encountered during the study. One solitary seedling grew on transect three and has cluster size and micro-habitat data included with other information from transect three. Three seedlings in a cluster (originating within a 0.5 cm diameter circle) were discovered by chance in the study area between transects.

Seedlings in unburned area. Only three solitary seedlings were found on transects six, seven, and eight, for a total transect length of 198 m through the live stand of krummholz whitebark pine. The seedling density ranged from 0.0/m^2 to 0.016/m^2 with a mean of 0.008/m^2 (Table 3). The seedling density was lower in the live stand of whitebark pine than in the burned tract ($P = 0.071$, Mann-Whitney U test) for an overall seedling density of 0.008/m^2. The heights of these seedlings, ranging from 2.5 cm to 11 cm with a mean of

TABLE 3. SEEDLING DENSITY, SEEDLING CLUSTERS, AND SEEDLING HEIGHTS ON TRANSECTS.

	Transects: burn					live stand		
Seedlings	1	2	3	4	5	6	7	8
Sites								
No. sites	7	6	5	9	4	1	2	0
No./m²	0.021	0.018	0.015	0.027	0.016	0.008	0.016	0
No. solitary	4	2	2	5	3	1	2	0
Cluster sizes	2, 2, 4	2, 3, 2, 2	2, 2, 3	3, 2, 3, 3	4	—	—	—
No./site (singles + clusters)								
Range	1–4	1–3	1–3	1–3	1–4	—	—	—
Mean	1.7	1.8	1.8	1.8	1.8	1	1	—
s.d.	1.1	0.8	0.8	1.0	1.5	—	—	—
Median	1	2	2	1	1	—	—	—
Heights (cm)								
No. seedlings	11	11	9	16	7	1	2	0
Range	1–8.5	1.5–10	1.5–2.5	2–13	2–8	—	2.5–11	—
Mean	3.4	4.2	2.0	5.3	3.6	7	6.8	—
s.d.	2.0	3.1	0.2	2.8	2.1	—	—	—
Median	3	3	2	4.5	3	—	—	—
Cluster area (cm) (diameter of area)								
No. clusters	3	4	3	4	1	—	—	—
Range	0–5	0–3	0–2	0–5	—	—	—	—
Mean	2	1	1	2.9	1	—	—	—

6.8 ± 4.0 cm, were significantly greater than those of the burn area ($t = 1.9$, $df = 55$, $P = 0.05$).

Seedling sites. Transects one through five provided information on the characteristics of those sites in which seeds germinated and survived. In conifers, the heaviest mortality occurs during the early stages of growth (Baker 1950).

For the 31 seedling sites surveyed, substrates were of various combinations of granitic gravel (partly crystalline and coarse), duff, mineral soil, and fine ash. The most common combinations are gravel alone—35%, gravel and duff—19%, and duff alone—16%. Fewer than 10% of all seedling sites contained ash. All of the seedlings were more or less sheltered by large rocks, as opposed to growing in the open: 48% of the seedling sites were 0 to 30 cm from a large rock ($\bar{x} = 8.4 \pm 8.5$ cm, median = 7 cm), 16% were in narrow crevices between large rocks, and about 36% were under rock overhangs. For the three seedlings encountered among live whitebark pine on transects seven and eight, micro-habitat characteristics followed the same trends.

Seedling ages. Cores from five whitebark pine trees in the burned areas, with trunk diameters ranging from 1.3 to 17 cm, had growth rings barely separable under a hand lens, confirming that krummholz whitebark pine, like other arid site conifers, is slow-growing (Fritts 1974). According to growth rings, a seedling 5 cm in height collected in the Cathedral Peak burn in August 1979 was three years old, for a mean height growth rate of ca. 1.7 cm/yr; whereas, a seedling 30 cm in height taken from the less extreme environment of Budd Lake (elevation 3050 m, ca. 1 km straightline distance southeast of Cathedral Peak) was 13 years old for a mean growth rate of ca. 2.3 cm/yr (J. W. van Wagtendonk, pers. comm.).

Fourteen whitebark pine seedlings that germinated in August 1975 on Mammoth Mountain (Tomback 1982) provide additional information for aging seedlings. They ranged in height from 2.5 cm to 5.7 cm with a mean, s.d., and median of 4.2 ± 1.2 cm and 4.0 cm, respectively. Mean growth rates ranged from 0.5 cm/yr to 1.1 cm/yr. In fact, although the mature trees adjacent to the seedlings were of the erect growth form, the local growing conditions are harsh, with deep snow pack, high summer temperatures, and water stress exacerbated by pumice substrate. The mean and median seedling heights recorded in the Cathedral Peak burn (Table 3) fit well within the height range of the Mammoth Mountain seedlings, although of the 54 seedling heights measured in the burn, 12 (22%) fall above the range. These 12 seedling heights are the consequence of either more favorable micro-habitats or pre-fire germination. The former possibility is supported by the 1.7 cm/yr rate reported for the seedling collected on Cathedral Peak in 1979. Thus, it is reasonable to assume in the absence of reliable ages that most of the seedlings surveyed germinated after the 1975 fire.

Seed sources. Few whitebark pine cones were available in or near the study area to provide a direct seed source for reforestation. The scattered patches of live trees in the burned area were non-productive in 1979. Of the 13 trees censused, none had cones of the current crop, and only two had cones of a previous year (Table 2). Although one tree at the top, south end of the burned area bore several whorls of ripe cones, no new cones were observed on any of the live trees on transects six, seven, and eight.

Data gathered on transects of the east- and lower west-facing slopes (Tomback 1981) are summarized here: on the east slope transect from 3050 m to 3250 m, 50% of the 36 trees surveyed bore no cones, 19% bore old cones and a few new cones, and the remainder bore only old cones. On the west slope transect from 3050 m to 3200 m, 43% of the 44 trees surveyed bore no cones, 39% bore old cones and a few new cones, and the rest bore only old cones. Thus, some of the whitebark pine trees on the east and lower west slope were potential seed sources for regeneration in some years.

Nutcracker activities. Nutcrackers occurred on the slopes and forested regions around the base of Cathedral Peak in August and September. Solitary nutcrackers and pairs occasionally flew over the burned study area to the east or west slope. By early August, nutcrackers were harvesting whitebark pine seeds in the Cathedral Peak environs for immediate consumption or for feeding dependent juveniles. Nutcracker-foraged cones are distinct in appearance: they are partly or completely hollowed out from one side. By 10 August, 59% of the new cones observed along the west slope transect had been opened by nutcrackers. In late August, nutcracker seed caching activities begin in the eastern Sierra Nevada (Tomback 1978). By 8 September, 100% of the new cones on the east slope transect had been foraged by nutcrackers (Tomback 1981).

On two separate occasions on 11 September, nutcrackers were observed burying seeds in the study area. The first nutcracker buried two seed caches in the burn and one or more additional caches in the adjacent live stand. The second nutcracker buried two caches in the burn and three in the live stand and then flew upslope and over to the east side of the peak.

Discussion

Data on seedling occurrence indicate that regeneration of the whitebark pine forest in the Cathedral Peak burn is underway. Observations and circumstantial evidence suggest that seed dispersal by Clark's Nutcracker is a primary source of the regeneration, whether or not all the seedlings encountered on the transects originated after the August 1975 fire. Probable sources of whitebark pine seeds for nutcrackers were stands on the east and west slopes of Cathedral Peak and the adjacent forests. Thus, the seedlings in the burned area were probably from parent trees of the erect growth form. Which growth form these seedlings will assume is an interesting question.

It is unlikely that seeds from cones of unburned krummholz whitebark pine were an important source of reforestation. The poor cone productivity in the vicinity of the burn seemed typical of the krummholz form of conifers. The seeds of krummholz conifers, including *P. albicaulis,* also have been found to have less germination capacity than do seeds produced at lower elevations because of differences in seed weight and seed fertility (Tranquillini 1979). With one or two exceptions, those cones produced around the burn were all or partly destroyed by foraging nutcrackers and chipmunks. If a few viable seeds escaped the foragers, however, it is conceivable that the cones might abscise, roll, disintegrate, and establish seedling clusters. Arguments against this possibility have been presented by Tomback (1981, 1982). No debris was evident near seedling sites, especially under rock overhangs where such material might remain undisturbed. The minor role of other vertebrates in the dissemination of whitebark pine has been discussed at length (Tomback 1978, 1981, 1982, Hutchins and Lanner 1982). The low seed productivity of krummholz pine makes significant dispersal by other vertebrates especially doubtful.

At 48% of the seedling sites in the burn, seedlings were in clusters of two to four individuals. Single seedlings and clusters are a logical consequence if one or more seeds of a nutcracker cache germinate. Many such clusters of different ages were evident on the west slope of Mammoth Mountain in 1975, an area used commonly by nutcrackers for seed caching (Tomback 1978, 1982). It is noteworthy that nutcrackers tend to store caches near objects such as rocks, logs, and the base of trees (Tomback 1978) and in fissures in rock faces (Tomback and Kramer 1980). All seedling sites in the burn were in crevices between rocks, next to rocks, or under rock overhangs, and thus concurred with previous observations of nutcracker cache site preferences. These site choices probably increased seedling survivorship rates by providing some shade during the afternoon hours—a critical time in view of the western slope aspect—and perhaps more moisture. High substrate temperatures are a major source of seedling mortality, particularly during the succulent stage when hypocotyl tissue at ground level can be literally 'cooked.' The mortality rate from heat injury is notoriously high on dry, sunny slopes (Baker 1950).

Many of the tree skeletons in the burn had more than one trunk, with the multiple trunks fused at the base, clear lines of separation between fused trunks, and distinctive wood grains in each trunk. This growth form resembles the multi-trunked erect form described and analyzed electrophoretically by Linhart and Tomback (1985). Using only two to four gene loci, they discovered that two or more trunks per multi-trunked tree were distinct genotypes, suggesting an origin in nutcracker caches. Until a similar analysis is applied to the 'multi-trunked' krummholz form of *P. albicaulis,* it can only be speculated that this form is also the consequence of seed dispersal by nutcrackers and not of stressful growing conditions. Support for this idea comes from the fact that the krummholz trees had one to five trunks per tree with a mean of 2.2, and seedling cluster sizes ranged from one to four with a mean of 1.7.

If all seedlings surveyed, with the possible exception of two, were established after the fire, then the time required to achieve a pre-fire population density can be estimated. The overall density of mature trees in the pre-fire forest was ca. 0.149 trees/m^2. In 1979, five summers after the burn, the overall density of post-fire seedling sites was ca. 0.020/m^2. If seedling survival rate is 25% (a liberal estimate: see Baker 1950, Tomback 1982), then at the current rate of afforestation, a maximum of about 150 years is required for restocking. It is important to note, however, that many seedling sites are occupied by clusters, and only some of the seedlings within clusters may die. Thus, not all mortality will decrease the rate of 'tree' recruitment. Although this factor decreases actual restocking time, it may be counterbalanced by post-seedling mortality. At some point, the rate of population recruitment may decline. Within the live krummholz pine stand on Cathedral Peak, the seedling density was lower than in the burned area. This may be a consequence of either higher seedling mortality in the forested area or of nutcracker preference for more open sites for seed caching. Regardless, as recruitment progresses, soil conditions and micro-habitats may change and alter regeneration rates.

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